STUDIES ON INHERITANCE IN PIGEONS. IV. CHECKS AND BARS AND OTHER MODIFICATIONS OF BLACK[1]

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INTRODUCTION

A considerable interest has for some time been attached to the evolutionary, and in later years to the hereditary, relationships of the two color patterns in pigeons, known as blue black-barred (figure 5) and check (figure 3). This was due, in part at least, to the probable universality of these two patterns in many of the old domesticated races. According to BUFFON (1793), for instance, ALDROVANDUS about 1599 described the pigeon of Crete as having a bluish plumage, "and marked with two blackish spots on each wing." The same authority quotes WILLUGHBY (1678) as giving a similar description for the pigeon of Barbary. MOORE (1735) occasionally mentions "blue" types among the several varieties listed by him, as for example the Spot, the Jacobin and the Helmet. Both blue and checked examples are referred to in the "Taubenbuch" (ANONYMOUS 1790). Though the descriptions of these early writers are too brief to show with certainty that the "blue" to which they allude is

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similar to the blue with black wing bars, or blue with black check-marks of modern breeds, there is nothing to indicate a reference to any other color.

Writers of the early and middle nineteenth centuries, as BOITARD and CORBIE (1824) and EATON (1858), also mention blue and checked varieties of several breeds, describing them in detail. Later DARWIN (1868, vol. 1, p. 197) listed several breeds in which these two color patterns were known to occur.

Of equal if not even more importance than the mere presence of barred and checked types in established breeds was the occasional appearance of these two patterns, not only in presumably "pure" stocks of other colors, as black or white, but also in crosses of various colored birds not having, so far as was known, any barred or checked individuals in their ancestry. Descriptions of some such crosses made by the writers just cited, are presented by them in some detail. It will be sufficient to state here, however, that special attention was called to the unexpected cropping out of birds with one or the other of the patterns under discussion. As late as 1909 the French writer BAILLY-MAITRE refers to blue as the fundamental color and calls attention to its unexpected occurrence in various stocks.

At the same time the presence of the barred pattern among different species of pigeons in widely separated geographic areas was noted and described. DARWIN (1868, vol. 1, pp. 182–184) and TEGETMEIER (1868, pp. 26–27) describe these various species. The first one is *Columba leuconata*, which is blue with three wing bars and inhabits the Himalayas; those with two wing bars are *C. livia*, found on the coasts of Scotland and England, and *C. rupestris* of central Asia. Similar to these are *C. schimperi*[2] of Abyssinia and *C. gymnocyclus* of West Africa. These and others are detailed by SALVADORI (1893). More might be enumerated but the above will suffice to show the prevalence of the blue black-barred pattern among various species of the Columbidae.

Checked varieties for each of these wild species are not mentioned, but they may nevertheless exist. Such a variety of *C. livia* is well known and Darwin (1868, vol. 1, p. 184) mentions a checked specimen of *C. schimperi* in the BRITISH MUSEUM.

Somewhat similar checked patterns are found in *C. guinea* and many of the doves (mourning doves, ground doves, etc.); in fact a large number

[2] The writer examined a blue specimen of *C. schimperi* belonging to the FIELD COLUMBIAN MUSEUM of Chicago and was struck with its similarity to our common blue pigeons. This specimen was from Egypt.

of the individuals of the order Columbae exhibit checks. Whether the genetic behavior of the checks of *C. livia* and of the doves are similar is as yet a question.

From a study of the above-named species and many more DARWIN was led to the belief that *C. livia* was the progenitor of the domesticated pigeon, since it resembles the domesticated varieties in form more closely than do the other species. But of equal importance is the fact that it is easily domesticated and proves to be fertile with and to produce fertile hybrids by the domesticated pigeon.

Granting *C. livia* to be the progenitor of the domesticated races DARWIN easily accounted for the reappearance of checked and barred birds in supposedly pure stocks and in certain crosses, as reversions to the ancestral type. It is still generally conceded that *C. livia* is the progenitor of the domesticated varieties, and geneticists also interpret the unexpected appearance of checked and barred birds as reversions, but they attribute them to factor recombinations (COLE 1914, p. 343).

After conceding *C. livia* to be the ancestor of the modern races of pigeons, the next step was to determine the relationships of the two patterns, check and bar, and to discover if possible which was the original. It is this question which has produced a certain amount of speculation and some experimentation from the evolutionary and genetical standpoints.

DARWIN believed the barred type to be the original, while checked birds were probably due to "the extension of these black marks [black bars] to other parts of the plumage" (DARWIN 1868, vol. 1, p. 183). WHITMAN, on the other hand, assumed the opposite view, namely that the barred type resulted from a gradual clearing of the wings of checks "from before backwards" (WHITMAN 1919, vol. 1, p. 19), until the two-barred type resulted. He went further and stated that the evolution of these types was an orthogenetic one, basing his conclusions on certain results which he obtained from selection experiments.

The above are the two main evolutionary views, which obviously contradict each other. The other way of ascertaining the relations of the two patterns is by Mendelian breeding methods applied both to domesticated varieties and to birds of the wild stock representing the two patterns. These genetic relationships have been fairly well established by STAPLES-BROWNE (1908, 1912) and BONHOTE and SMALLEY (1911), who advanced data showing the independent Mendelian inheritance of the two patterns.

In view of the foregoing, the object of this paper is to show the hereditary relationships of the two types under consideration to the other colors in pigeons, with special reference to black; secondly, to show from a microscopic study of pigment arrangements and breeding experiments the interaction of several factors affecting blue and black; and lastly to interpret WHITMAN's results on a genetic basis.

The data which follow are taken not only from special matings made by the writer at the WISCONSIN AGRICULTURAL EXPERIMENT STATION during a period of three years, but also from the entire set of pigeon records dating back to the beginning of the work by Professor COLE at the RHODE ISLAND STATION in 1907. As a consequence many of the matings used by him in his 1914 paper and also in the 1919 paper by COLE and KELLEY are repeated here.

THE "BLUING" SERIES

There is a wide range in the amount of blue which may occur, from full black, where no blue at all is present, to a type known as barless, in which nearly the whole bird is blue. The variations form a series of gradations of increasing "bluing." The six types which have been distinguished in this work are fairly distinct, though there is some intergrading in certain cases. The breeding behavior, however, seems to indicate their genetic distinctness. It is probable that the intergrading is due, in some cases at least, to modifying factors of one sort and another; and it is also not improbable that other genetically distinct grades may exist besides those described. These six types are described in the order of their progressive bluing (decreasing amount of black in relation to blue), and it is interesting that they appear to be epistatic in their hereditary manifestation in the same order, i.e., each to the one that follows. It is to be noted that blue appears in the rump and in the outer vanes of the outer tail feathers independently of this series.

"Full black" (figure 1) as used in the present paper refers merely to the absence of blue everywhere except in the rump and outer vanes of the outer tail feathers. Blue appears first in the tail, making the "black blue-tail," and its further invasion results in the "checked," "sooty," "blue black-barred" and "barless" types, all of which, however, have the characteristic blue tail. Full black takes no cognizance of kitiness (reddish), often present in the flights of black pigeons, nor of white spotting, nor, as mentioned above, of a dark blue rump or light outer vanes of outer tail feathers. A bird might possess all these characteristics, but so long as it lacked the blue tail with black terminal band it would be classified as a full black.

"Black blue-tail" is the next stage below full black. The chief distinguishing characteristic from black is the blue tail with a black terminal band. This pattern shows variability in itself, since all birds entirely black except for blue tails (figure 2) to those with blue or almost white rumps and with or without some bluing in the primaries, but with unchecked wing coverts are included in this class.

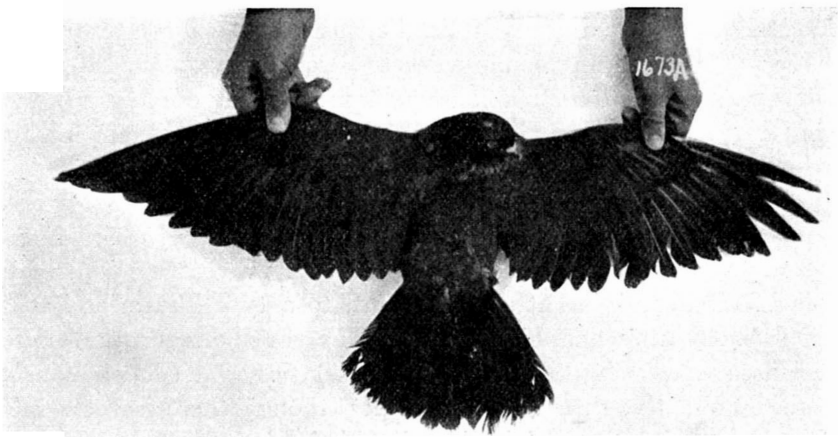

FIGURE 1.—Full black with uniform rump (grade 5) and uniform outer vanes of outer tail feathers. (Wisconsin No. 1673A.)

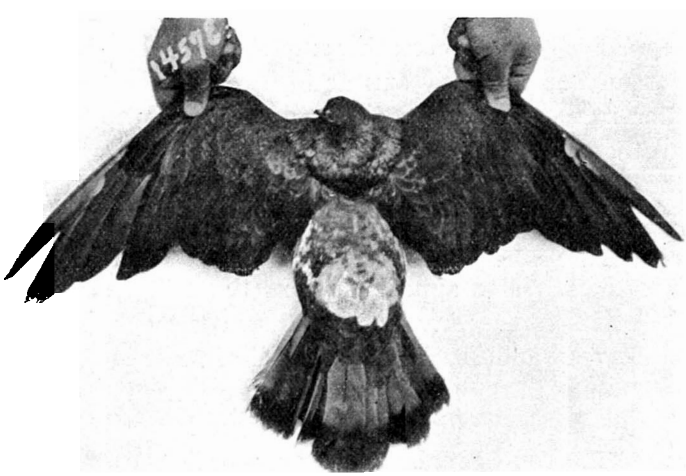

FIGURE 2.—Black blue-tail with uniform blue rump (grade 3) and light outer vanes of outer tail feathers. The white feathers in the rump are not considered. (Wisconsin No. 1457E.)

References to this type are not very numerous. DARWIN (1868, vol. 1, p. 184) in describing the Rock Pigeon of Madeira says, ". . . others are chequered, like *C. affinis* from the cliffs of England, but generally to a greater degree, being almost black over the whole back; . . . . ." The "reversionary blues" described by STAPLES-BROWNE (1908, 1912) belong in this class.

"Check" originates from the so-called checked appearance of the wing (figure 3). This condition is caused by the presence of two black marks situated respectively in the inner and outer vanes of the wing coverts, the central and proximal portions of which are blue. The rest of the plumage of checked birds is blue with the invariable exception of a

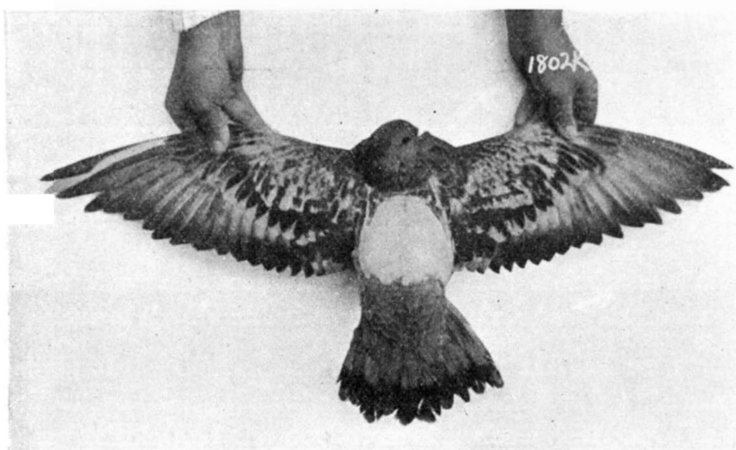

FIGURE 3.—Medium check with extreme light blue rump (grade 1); outer vanes of outer tail feathers only slightly lighter than those of the other tail feathers. (Wisconsin No. 1802K.)

black terminal band on the tail and of the not infrequent presence of checks on the upper back. The rump may be either very light, almost white, or a shade of blue uniform with that of the wing coverts, or any shade between these two colors.

"Sooty" is the fourth variation of the bluing series to be considered. The black blue-tail represents a character which is blacker than the check, while the sooty character is representative of the opposite condition. Sooty, as the name implies, comprises those individuals whose wing coverts have a mere sprinkling of black, giving the bird a sootied appearance (figure 4). The black on the wing coverts is so small in amount that it fails to take on a definite pattern as it does in the typical check.

It is not at all difficult to differentiate between sooty and check, as the sprinkling of black on the wing coverts is easily distinguished from the definite black spot of the check mark.

References to this type are also few. CHAPMAN (1911, p. 5) mentions sooty blues. STAPLES-BROWNE (1912) in describing the offspring from the Rock-Fantail cross says that the classification of birds into "chequered" and "non-chequered" groups was complicated by several individuals which he termed "intermediates" and described "as showing a slight darkening of some of the lower wing coverts, which is not noticeable unless the bird is caught." This description is in keeping with what is referred to as sooty in the present paper. Although WHITMAN does not

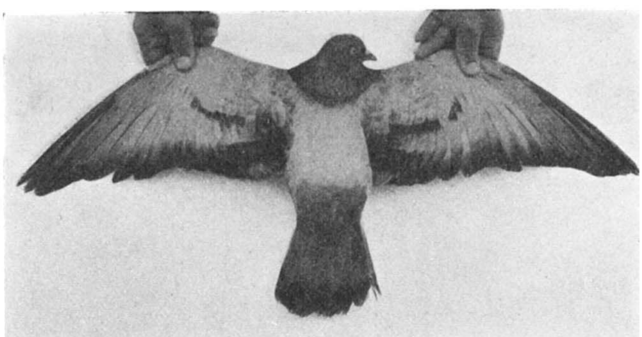

FIGURE 4.—Sooty blue with light blue rump (grade 2) and light outer vanes of outer tail feathers. (Wisconsin No. 1777A.)

definitely discuss this character, the plate of *C. oenas* (WHITMAN 1919, vol. 1, plate 9) appears to depict the character very well.

"Bar" refers to the pattern commonly called "blue black-barred." The wings of a barred bird are blue with two transverse black wing bars, one of which extends through the tertiaries and innermost secondaries, while the second extends through most of the secondary coverts (figure 5). The so-called blue of the pigeon is in reality a gray which, according to COLE (1914), corresponds to RIDGWAY's "gull gray." The tail and rump are similar to those of the check, but the back is free from any check marks.

"Barless," the sixth and last variation, is, so far as known at present, the lowest stage in the bluing series. As the name implies, the wings lack any bars, which makes the distinction between this type and bar very easy. In the barless individual the so-called blue has entirely replaced the black wing bars leaving a clear blue wing, except for the darkened tips of the primaries, secondaries and tertiaries.

This character has been known for some time. DARWIN (1868) mentions as barless a sub-variety of the Swallow, of German origin, pictured by NEUMEISTER. LYELL (1887) calls attention to the same pattern in the Ice Pigeon and a variety of the Swiss Pigeon. SCHACHTZABEL (1906) pictures several barless varieties as follows, the Strasser, Goldgimpel, (which has a yellow body and blue barless wings), the Pfaffen and Eichbuhlertaube. BAILLY-MAITRE (1909) also names a barless variety of German origin, "Feld-Tauben." Both the barless Strasser and Ice Pigeon as well as barless varieties of the Swallow and Homer are produced in this country. Figure 6 represents the latter breed.

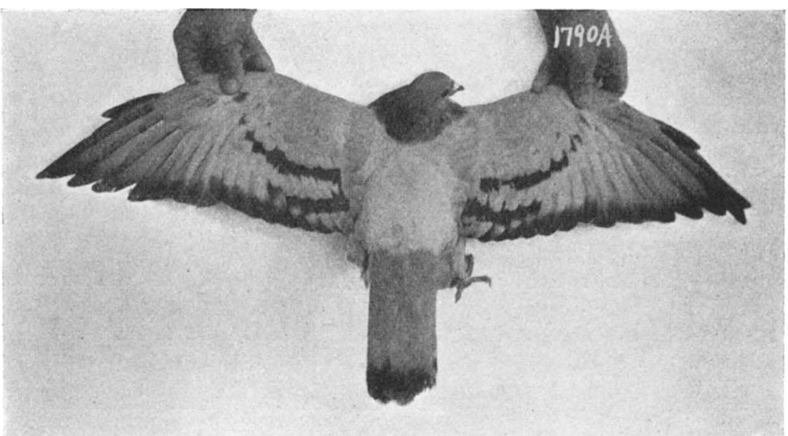

FIGURE 5.—Blue black-barred with light blue rump (grade 2). (Wisconsin No. 1790A.)

Genetic relationships of black, check and bar

The phenotypic differences between these three characters depend upon the presence of varying amounts of the two so-called colors, black and blue, the check being the intermediate type. A further difference between the two colors is one of pigment-granule arrangement. COLE (1914) showed these granules in the barbules of a black feather to be evenly distributed and those in a blue feather to be clumped. These two conditions have been found, as might be expected if checks are a combination of black and blue, existing side by side in the feathers of checked birds. It is this difference in pigment arrangement that produces the two different optical effects.

COLE also showed that full black is dominant to the barred type. In view of the microscopic study just discussed he postulated a factor *S* which referred to the spreading of the pigment granules evenly throughout the barbules of black feathers, while *s* indicated the clumped condition in blue ones. Table 1 is presented as furnishing further data on the dominance of black birds known to be *SS* to bar (*ss*). From three such

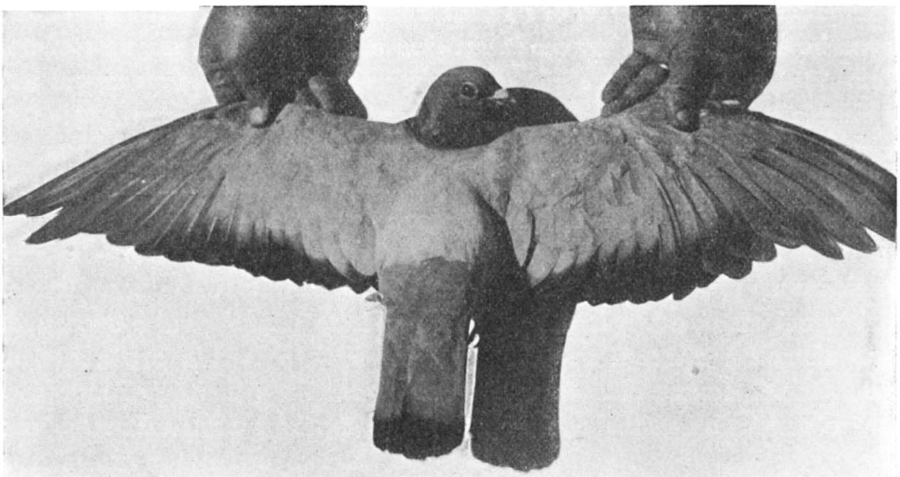

FIGURE 6.—Blue barless Homer with light blue rump (grade 2). (Wisconsin No. 1751A.)

matings 22 full-black offspring resulted. COLE's data and those of the writer regarding the segregation of the *S* factor will be presented and discussed later. It may be stated here, however, that black differs from bar by a single factor.

TABLE 1
Black (SS) by bar (ss).

MATING	♂♂	COMPOSITION	♀♀	COMPOSITION	OBSERVED S-BLACK	EXPECTED S-BLACK
1033	999A	*sscc*	7A	*SS(CC)**	10	10
1746	1671A	*SS(CC)*	1470F	*sscc*	7	7
1803	1462H	*SS(CC)*	1670A	*sscc*	5	5
Total	(3 matings)				22	22

* Letters inclosed in parentheses indicate uncertainty as to this portion of the formula.

The next step was to establish the relation of black to check. Since the black birds in the colony at the WISCONSIN STATION were known to be heterozygous for various color characters including those for check and bar, the purchase was made of several black Tumblers, presumably "pure" for black, that is, not having any barred or checked ancestry. The checked parents were from colony stock and were known to be heterozygous. The breeding results proved the blacks purchased to be homozygous, and it is obvious that black is dominant to check, since in six matings 57 full-black birds were obtained, and as many as 22 in a single mating (1686).[3]

When two blacks homozygous for S, or when at least one parent is of this composition, are mated together, only full blacks result. Six such matings gave a total of 61 full-black offspring.

That there is apparently a single-factor difference between black and check is shown by the very close 3 : 1 ratio obtained in table 2. Five matings of full-blacks to full-blacks when both were known to be heterozygous give a total of 25 blacks to 8 checks, the expected being 24.75 to 8.25.

TABLE 2

Segregation of S and s in presence of CC.*

MATING	♂♂	COMPOSITION	♀♀	COMPOSITION	OBSERVED		EXPECTED	
					S Black	C Check	S Black	C Check
554+	450X	$SsC(C)$	450Y	$SsC(C)$	6	1	5.25	1.75
662+	493B	$SsC(C)$	454B	$SsC(C)$	8	1	6.75	2.25
1015+	790B	$SsC(C)$	799A	$SsC(C)$	4	1	3.75	1.25
1025+	862A	$SsC(C)$	$862B_3$	$SsC(C)$	3	3	4.50	1.50
1812	1685C	$SsC(C)$	$1594Q_3$	$SsC(c)$	4	2	4.50	1.50
Total	(5 matings)				25	8	24.75	8.25

* Only those matings from which 5 or more offspring resulted, and only those for which complete descriptions were made, have been used in the compilation of this table.

Having shown black dominant to both check and bar and differing from each by a single factor, the relation of check to bar will next be discussed. BONHOTE and SMALLEY (1911) state that they have accurate records on fifty-seven matings of check by check, from which 229 checked offspring resulted. Reference to the work of STAPLES-BROWNE (1912) gives one mating of check by check producing ten offspring which,

[3] Many of the tables giving detailed results of individual matings have been omitted from this paper in order to economize in the cost of printing. They will be found in full in the original thesis deposited in the Library of the UNIVERSITY OF WISCONSIN.

according to the author, indicates that at least one parent was homozygous for check. He also presents a mating of check by bar giving eight checked squabs, indicating the dominance of check to bar. Similar data are available from WHITMAN (1919, vol. 2, table 72, p. 104). Two checked wild Rocks produced 16 checked offspring and no barred, showing without doubt that one parent at least was homozygous for check. In the present experiments a mating (1607) of homozygous check by bar gave 8 checked offspring and two others (1596, 1743) of a black blue-tail male, known to be homozygous for C, with barred females produced 12 check and 2 black blue-tailed progeny. This male must have been heterozygous for black blue-tail. These and the earlier results demonstrate that checks (or black blue-tails) homozygous for C, when mated to checks or bars, do not throw individuals lower in the series than checks.

Data on the segregation of the factor for check are also numerous. STAPLES-BROWNE gives three matings of check by check in which both parents are heterozygous. The result of these matings was 21 check to 12 bar, which is not very close to a 3:1 ratio. BONHOTE and SMALLEY (1911) give two similar matings from which 13 checked and 4 barred offspring were obtained, which numbers are very close to the above ratio. The work of NUTTAL (1918) might offer some available material on this point if the matings had not been complicated with the known sex-linked A-factor which restricts black, and possibly with others. WHITMAN (1919, vol. 2, table 72, p. 104) obtained from two matings of checked birds, presumably heterozygous judging from the patterns of the progeny, 23 checked offspring and 5 barred. One of the parents of one mating was procured from a fancier and the other parent was a stray pigeon, while the parents of the second mating were both original wild Rocks from the Cromarty caves of Scotland. These figures also, considering the numbers, fit a 3:1 ratio fairly closely. Eleven matings made by the writer, in which checked birds heterozygous for this factor were interbred, gave 59 checked (excluding 1 possible black blue-tail) to 18 barred offspring. This is very close to a 3:1 ratio (57.75 : 19.25). A summation of the foregoing results gives 116 checked to 39 barred birds, where the expectation is 116.25 to 38.75, seeming to demonstrate that check and bar differ by a single Mendelian factor.

Further data, from matings in which 1:1 ratios are expected, are available from STAPLES-BROWNE and WHITMAN. The latter presents two such matings giving 9 checks to 10 bars, and the former (STAPLES-BROWNE 1912) two matings which give 5 checked to 18 barred offspring. The results of the last two matings are certainly not very close to expectation. A tabulation of twenty-one matings of heterozygous checks mated to bars, exhibits a fair 1:1 ratio (87:105).[4] $\frac{\text{Deviation}}{\text{Probable error}}\left(\frac{.09}{.05}\right)=1.80$ indicates that the discrepancy may be due to random sampling.

Blacks, then, throw blacks, checks, and, as will be shown presently, also bars, while checks throw only checks and bars. Bars, however, produce neither blacks nor checks but bars only, as is shown by the following results obtained from many matings in several stocks of bars to bars. BONHOTE and SMALLEY (1911) secured from twelve such matings 41 barred offspring, STAPLES-BROWNE (1912), 198 barred birds, and WHITMAN (1919), 16 barred individuals from six matings of barred wild Rocks. The writer's data show that forty-nine barred offspring resulted from six matings of bar to bar and one mating of bar to barless (1770). Three hundred and four barred birds have, accordingly, been obtained from at least four entirely different stocks constituting 53 different matings of bars to bars, which shows fairly conclusively that barred birds breed true.

In order to explain the foregoing results a factor C for check has been postulated. It is not linked with S but can act only in the presence of s to produce the checked pattern. In other words S is epistatic to C. When neither S nor C are present the barred type is the result. Blacks, then, may or may not carry C and can consequently be of the following compositions, $SSCC$, $SSCc$, $SScc$, $SsCC$, $SsCc$, $Sscc$. Checks, on the other hand, can be of but two sorts, $ssCC$, $ssCc$, while the barred type can be only $sscc$.

In order to further illustrate such a hypothesis the data in tables 3 and 4 are presented. Table 3 shows four matings of blacks by blacks heterozygous for S and C, in which case a 12:3:1 ratio is expected. The total for each of the three classes for which complete descriptions are given is small (15:6:4). As a consequence the closeness of fit (P) is poor (.086). When, however, all individuals are included the ratio becomes 25:6:4 and the value for P is then .461 which is a fair fit. The matings of table 4 consist of black birds heterozygous for S and C, mated to bars, which give an expected ratio of 2:1:1. The check class is low and the bar class high. Consequently the value for P (.154) can hardly be called fair. It is reasonable to suppose that the low values for P are due to the small numbers from which they are calculated and not to a misinterpretation of the data.

[4] The 105 bars include 4 sooty birds, which can be legitimately included in the present instance, however, as "non-checks."

TABLE 3

Blacks (SsCc) by blacks (SsCc).

MATING	♂♂	COMPOSITION	♀♀	COMPOSITION	OBSERVED			EXPECTED			NOTES
					S Black	*C* Check	*Ba* Bar	*S* Black	*C* Check	*Ba* Bar	
1296	1033A	*SsCc*	1033B	*SsCc*	4	2	2	6.0	1.5	.5	2 blacks not included, poor descriptions
1305	1033D	*SsCc*	1033E	*SsCc*	7	2	1	7.56	1.89	.63	3 blacks not included, poor descriptions
1110+ and 1332	905B	*SsCc*	864A	*SsCc*	2	1	1	3.00	.75	.25	4 blacks not included, poor descriptions
1126+ and 1311	962A	*SsCc*	915B	*SsCc*	2	1		2.28	.57	.19	1 black not included, poor description
Total (4 matings)					15	6	4	18.72	4.68	1.56	$\chi^2=4.924$ P=.086
Total all birds included					25	6	4	26.28	6.57	2.19	$\chi^2=1.609$ P=.461

TABLE 4

Black (SsCc) by bar (sscc).

MATING	♂♂	COMPOSITION	♀♀	COMPOSITION	OBSERVED			EXPECTED			NOTES
					S Black	*C* Check	*Ba* Bar	*S* Black	*C* Check	*Ba* Bar	
1448	1341D	*sscc*	915B	*SsCc*	8		4	6.00	3.00	3.00	2 not used
1454	1385B	*SsCc*	1242A	*sscc*	6		4	5.00	2.50	2.50	1 not used
1484	962A	*SsCc*	1432A	*sscc*	1	2	2	2.50	1.25	1.25	
1681	1512R	*SsCc*	1657Z	*sscc*	1	1	2	2.00	1.00	1.00	1 not used
1682	1448T	*SsCc*	1668A	*sscc*	4	5	4	6.50	3.25	3.25	
1742	1666G	*sscc*	1454V	*SsCc*		1	2	1.50	0.75	0.75	
1748	1657J	*sscc*	$1616A_2$	*SsCc*	5	1	1	3.50	1.75	1.75	
1767	1532D	*sscc*	1699Q	*SsCc*	7	3	5	7.50	3.75	3.75	
1824	1659S	*sscc*	1605V	*SsCc*	2	1	1	2.00	1.00	1.00	
1859	$1553J_2$	*SsCc*	1657Z	*sscc*		1	1	1.00	0.50	0.50	
Total (10 matings)					34	15	26	37.50	18.75	18.75	

$\chi^2=3.782$ P = .154.

The description of the inheritance of these three patterns corresponds somewhat to that offered by COLE (1914) for the occurrence of STAPLES-BROWNE's "reversionary blues." COLE suggested a factor T which, like the C factor, acted only in the absence of S. He also pointed out that the blues which STAPLES-BROWNE recovered from his second generation of black Barb and white Fantail cross were not the same as those to which DARWIN referred. These birds instead of having clear blue wings with two black wing bars as described by DARWIN and referred to in this paper as the barred type, had black wings with indistinct blacker bars and blue tails with black terminal bands. In offering such an explanation for STAPLES-BROWNE's data, COLE differentiated between typical full blacks and blacks with blue tails, as the writer has done for blacks and checks, but in presenting his own data on the segregation of the S factor all black blue-tailed birds and also checks were included in one class with the full-blacks, while the typical blue black-barred birds were put in the other class. Data have been presented to show that blacks and checks differ by the S factor and more data will be given later to show that black blue-tailed birds do not carry S. Consequently the S factor as presented here differs from that postulated by COLE for his own data, but corresponds to that offered by him in explanation of STAPLES-BROWNE's findings. According to the present interpretation it refers only to full-blacks, while all black blue-tailed and checked birds are the result of its allelomorph (s) plus two other factors, T and C. On such a hypothesis COLE's data showing the segregation of S should better fit a 15:1 ratio than a 3:1. While his numbers (19:3) based on the offspring from three matings are too small to prove this point one way or the other, they at least fit a 15:1 ratio quite as well as a 3:1.

The epistatic series, black, black blue-tail, check, sooty, bar and barless

The relation of black to check and bar has been discussed. It is now proposed to consider the other members of the series.

Data giving the complete Mendelian inheritance of black blue-tail are insufficient. What there are, merely show that it appears to behave toward black very much as does check. Seven matings of blacks to blacks which throw black blue-tail, gave 21 of the former to 9 of the latter. It may be assumed that these blacks were heterozygous for S and homozygous for T, the factor determining black blue-tail, since they produced no offspring lower in the series. This result is suggestive of a single-factor difference.

Various matings of black blue-tail to other types in the series are given in sections A, B, C and D of table 5. In the later sections are various combinations of other types lower in the series. The numbers in most cases are too small to have much significance as to ratios, but it is to be noticed that in general the results confirm the conclusion that in any mating offspring are not produced higher in the series than the high parent. The one or two exceptions will be discussed below. In many of the matings there were offspring which died too young for description, or which were for other reasons insufficiently described; these might have changed the ratios materially.

Section A consists of two matings of blacks by black blue-tails. Three types are produced, blacks, black blue-tails and checks. In section B there is an exception to the rule that the grade of the offspring is not higher than that of the parents, for a pair of black blue-tail birds have produced three full-black offspring. By hypothesis black blue-tails do

TABLE 5

Matings of blacks, black blue-tails, checks, sooties and bars.

MATING	♂♂	COMPOSITION	♀♀	COMPOSITION	*S* BLACK	*T* BLACK BLUE-TAIL	*C* CHECK	S_o SOOTY	B_a BAR
			A. Black by black blue-tail						
168+	28B	*SsTtC(C)*	71A	*ssTtC(C)*	3	1	6		
1076+	841A	*ssTtC(C)*	799B	*SsT(T)*	1	1			
			B. Black blue-tail by black blue-tail						
1592	1457E	*ssTtC(C)*	1457N	*ssTtC(C)*	(3)	2	2		
			C. Black blue-tail by check						
808+	194B	*ssTtC(C)*	559A	*ssttC(C)*			4		
1610	1457Q	*ssTtC(C)*	837B	*ssttC(C)*			2		
1694	1533V	*ssTtCc*	1607W	*ssttCc*			3		1
			D. Black blue-tail by bar						
1596	1533K	*ssTtCC*	1448E	*ssttcc*			6		
1608	1533V	*ssTtCc*	1472Q	*ssttcc*			12		
1743	1533K	*ssTtCC*	$1443C_2$	*ssttcc*		2	12		
1744	1533V	*ssTtCc*	1454M	*ssttcc*		1	3		
			E. Black by bar throwing sooty						
1472	829B	$Ss(TT)$ CcS_os_o	1296N	$ssttccs_os_o$	5		1	3	2

MATING	♂♂	COMPOSITION	♀♀	COMPOSITION	S BLACK	T BLACK BLUE-TAIL	C CHECK	S_o SOOTY	Ba BAR
			F. Check by bar throwing sooty						
30+	26A	$ssttccs_os_o$	27A	$ssttCcS_os_o$			6	1	8
1453	1077A	$ssttccs_os_o$	1196A	$ssttCcS_oS_o$				1	2
1652	1526H	$ssttCcS_os_o$	1443C[2]	$ssttccs_os_o$			4	2	1
1802	1704E	$ssttCcS_os_o$	1788A	$ssttccs_os_o$			3	1	2
Total (4 matings)							13	5	13
Expected (2:1:1 ratio)							15.5	7.75	7.75
			G. Check by sooty						
1342	1091J	$ssCc(S_o)$	1173A	$ssccS_o(s_o)$				1	
1765	1708B	$ssccS_o(s_o)$	$1607B_2$	$ssCc(S_o)$			6	5	1
1760	1657T	$ssCc(S_o)$	1652B	$ssccS_os_o$			1	1	1
1759	$1638D_2$	$ssC(CS_o)$	1173A	$sscc(S_o)$			1		
			H. Sooty by sooty						
1482	1385A	$ssccS_os_o$	1173A	$ssccS_os_o$				2	2
			I. Sooty by bar						
1664	1462H	$ssttccs_os_o$	1491D	$ssttccS_os_o$				3	4
1798	1777A	$ssttccS_os_o$	1665B	$ssttccs_os_o$				1	2
1669	1568U	$ssttccS_os_o$	1668A	$ssttccs_os_o$				1	4
Total (3 matings)								5	10

not carry S and hence should not produce blacks. It so happens, however, that the preponderance of the data presented in substantiation of the theory on the genetic relations of the various blue types to black are taken from matings of Homers and Tumblers, while these three exceptions occurred in a single mating of a pair of Fantails. It seems possible, therefore, that this breed may carry some modifying factors which disturb the usual relations.

Such a presumption is further substantiated when the several matings of black blue-tailed Tumblers and Homers to checks and bars of the same breeds (sections C and D) are considered. In seven such matings 46 offspring were produced and none was full black. Full-black, then, may carry the factor for black blue-tail (T), but black blue-tails, when bred to bars or checks, do not (with the exception above) throw full-blacks, that is, they do not produce offspring with more black than they themselves show.

The typical check is the next stage lower in the series. The distinction between check and black blue-tail is not as readily made as between full-black and black blue-tail. It is often difficult to differentiate between a very slight check (figure 11C) and a black blue-tail, as some birds have only a very little checking in a few of the greater wing coverts. In this case the classification has to be arbitrary, and for present purposes those birds with any checking on the wing coverts are considered as checks.

The breeding behavior of check, as already intimated, is similar to that of black blue-tail. In eleven matings of typical checks to checks (see page 476) only checks were produced, with one doubtful exception in which two slight checks produced a black blue-tail.[5] The squab died young, however, and at this time showed two shades of black instead of black and blue. Had it lived to maturity it might have moulted to a typical check, the poor black becoming at least somewhat blued. In the twenty-one matings of checks to bars (page 477) no offspring with more black than that shown by the checked parents resulted.

The writer's data on the Mendelian behavior of the sooty character are meager, as they were for the black blue-tail pattern. Nevertheless, they illustrate the same point. Sections E and F of table 5 show that full-blacks and checks when bred to blues may throw sooties. The numbers obtained in section F are, so far as they go, in fair accord with the present hypothesis. The checked parents are *Cc* and carry the factor for sooty in a heterozygous condition (CcS_os_o), for they throw sooties when bred to bars which lack both check and sooty (ccs_os_o). In this case a 2:1:1 ratio is expected. There is a preponderance of blues, which, however, may be due to the fact that the early descriptions made for the birds of mating 30+ were not as detailed as were the later ones for the other matings, and consequently, some of the 8 barred birds might be sooties. Section G gives the results of breeding sooties to checks, in which case sooties and checks are recovered. When sooty is bred to sooty or to bar (sections H and I) only sooties and bars result, no checks or forms higher in the series than the sooty being obtained. A 1:1 ratio is expected from the matings given in section I. There is a decided preponderance of blues, which is attributed to small numbers.

Bar, the fifth in the present series, has already been discussed in detail. It is easily differentiated from sooty and check by a complete absence of any black on the wings except the black bars. This type, it may be remembered, bred true; it did not produce offspring with more black than shown by the two wing bars.

[5] It is possible that the arbitrary point of demarkation referred to in the preceding paragraph may be genetically wrong and that these *slight* checks are really black blue-tails.

All that can be said at this time regarding the inheritance of barless is that it is apparently recessive to bar. A barred Homer crossed on a barless Homer gave four barred offspring and one which died before the wing bars developed, that is, before they normally develop in pure barred stock. In another mating the male was black but known to be heterozygous for S and to carry the factor for barring. The female was a barless Swallow. Only three offspring resulted, of which two were blue with black bars and one was a full-black with blacker bars. The data, though very few, nevertheless indicate that barlessness (b_a) is recessive to bars (B_a). No F_2 data have as yet been obtained, but there is every reason to believe that either complete segregation or at least a series which will show no more black than the blue black-barred grandparent, will result.

As has been frequently pointed out the blacker types throw individuals of various lower but not of higher grades. For instance, blacks may throw blacks, black blue-tails, checks, sooties and bars; black blue-tails (with one exception) throw black blue-tails, checks, sooties and bars; and so on, down the series.

Apparently, then, these six characters form an epistatic series illustrated in figure 7. This relation of several factors might naturally suggest multiple allelomorphs. They do not, however, fall into this category, since blacks known to be heterozygous for bar, when bred to bars, have produce checks (table 4, page 479), which is inconsistent with the theory of multiple allelomorphs. Furthermore, if these factors formed a multiple-allelomorph series no more than 3 types could ever be recovered from any one cross. On the epistatic-series interpretation it should undoubtedly be possible, however, to obtain the six types of the present series from suitable crosses, and 4 have actually resulted (table 5, section E) in a cross of a black by a bar.

So far as the data go the various factors are apparently not linked, but each is carried on a separate pair of chromosomes. Furthermore, these several factors do not have a cumulative effect as in quantitative inheritance, but each is capable of producing its particular effect in the absence of the ones higher in the series.

This series pertains to the orderly relation of various conditions of one character, these conditions being due to factors not allelomorphic to any of the other factors. Obviously, such an epistatic series cannot, as BREITENBECHER (1921, p. 66) suggests in his paper on multiple allelomorphs in Bruchus, also form a multiple-allelomorph series.

The epistatic series is of special interest in the light of WHITMAN'S selection experiments. He was able to select for fewer and fewer checks until he obtained a typical blue black-barred wing and finally one even without bars, but he was unable to reverse the process. These results led him to believe that the check pattern had probably evolved in an

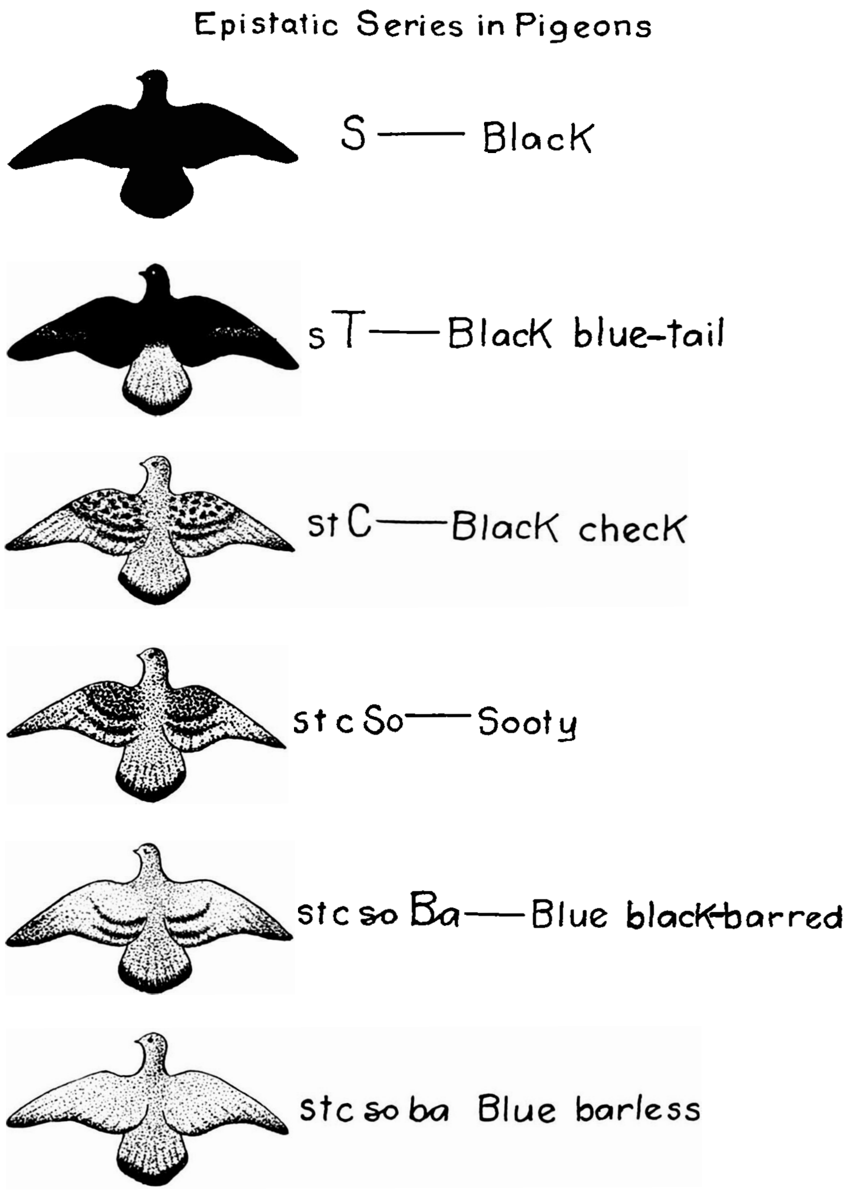

FIGURE 7.—Six distinguishable grades of the epistatic series showing the successive decrease in the amount of black (spread pigment) in relation to blue (clumped pigment).

orthogenetic fashion and that this type of evolution was continuing. His results, however, are quite in keeping with the genetic behavior of the factors in the epistatic series just discussed. Obviously mere heterozygosis is sufficient for obtaining the lower grades of check and bar, while it is very apparent that the higher grades can only result from dominant mutations. This would account for WHITMAN'S failure to obtain offspring with much checking from parents with only a little.

If the wild Rock is the progenitor of the domestic races of pigeons it seems evident, then, that black and black blue-tail have occurred by dominant mutations.

Relation of the factors, S, T, C, and S_0, to other known heritable colors

COLE (1914) showed that the S factor could be carried by red and yellow individuals. In other words the presence of B, the factor producing black pigment,[6] was necessary for the manifestation of S. In a similar way the presence of B is necessary for C to act, but S as already pointed out, must be absent. The same is true of the T and S_0 factors. Seven matings in which reds were mated to bars produced blacks, checks, sooties and bars, obviously showing that these reds carried S, C and S_0. If more birds had been tested, no doubt some carrying T would have been found. Nine matings of yellow and bar proved that yellows also transmit these four factors.

The C factor is carried in a similar way by whites, as shown by various crosses made by STAPLES-BROWNE (1912) of bars on whites with the result that the offspring were frequently checked. There is no reason to suppose that others with S, T and S_0 do not also exist.

The six patterns discussed are distinguishable in the dilute series as in the intense. That is, parallel to the first five grades of the intense series there are full-duns, dun silver-tails, dun checks, sootied silvers and silvers with dun wing bars. By analogy there should also be silver barless. Difficulty was sometimes found, however, in differentiating these dilute types because of the variations in the shades of dun. Many full-duns, that is, S birds, may have darker terminal bands on their tails, which complicates the usual easy distinction between S, T and C birds in the intense series, since the tails of the latter are as a rule uniformly black without a blacker terminal band.[7] In questionable cases of the dilute

[6] The action of B may perhaps better be considered as *extending* black pigment, making it analogous to E in mammals (see COLE and KELLEY 1919, footnote 4, p. 186).

[7] Two individuals of the SI type have been noted among the 1920 offspring, as having a darker terminal band with a lighter area just posterior to it. This area has somewhat of a bluish cast. When examined microscopically, however, it shows only clumped pigment as does the corresponding area in duns (Si).

series a microscopic study of that part of the tail anterior to the band, where clumped pigment is expected in checked and barred birds, was often necessary.

The next consideration was to correlate, if possible, the grades of the epistatic series with the various shades of red and yellow produced by the sex-linked black-restricting *A* factor. This, however, proved impossible with the present knowledge of the many variations of color due to this factor. There exist the so-called red-barred and red-checked types, but it was sometimes found upon testing that these did not always correspond to what was meant by check and bar in the *a* series. It is plain that the only way to determine the corresponding patterns in the two series is to test the many varieties of the *A* series by breeding to *a* bars. Until such work has been done an attempt to distinguish the *A* epistatic series will be postponed. Preliminary experiments demonstrated that *A*-factor birds may carry *S*, *C* and S_o. If more individuals had been tested, some carrying *T* would no doubt have been isolated as well.

While, then, the factors which produce the various grades of the *a* epistatic series can act only in the presence of *B* and absence of *S*, they can be carried by *b* and *S* individuals, by whites and by restricted reds. In other words they may be present in any of the eight known heritable colors of pigeons, but can not show except under certain favorable factorial conditions.

UNIFORM AND LIGHT OUTER VANES OF OUTER TAIL FEATHERS

The variation in the color of the outer vanes of outer tail feathers represents another modification of blue and black. Anyone familiar with pigeons is acquainted with the so-called light outer-vane condition found in both blue- and black-tailed birds (figures 12 and 2). It is restricted to that part of the outer vanes of the outer tail feathers proximal to the region occupied by the black terminal band characteristic of blue-tailed birds. This entire region or only the outer edge may be affected. DARWIN and LYELL call attention to it in descriptions of various breeds of pigeons, especially the wild Rock. The contrasting condition, uniformity, refers to the fact that this portion of the outer vane is similar in color to the other tail feathers, that is, in *S* or black-tailed birds it is black (figures 1 and 8A) while in blue-tailed or *s* birds it is blue (figures 9 and 8C).

A microscopic examination of the two conditions, uniform outer vane and light outer vane, in *S* birds (full-black, with black tails) shows them to be different. The pigment in the former (figure 8A) is spread, while in the latter (figure 8B) it is clumped. The uniform outer vanes of blue-tailed individuals (figure 8C), however, show clumped pigment. This is to be expected, since the factor *s* has already clumped the pigment and, as mentioned above, uniformity merely means that the outer vanes shall

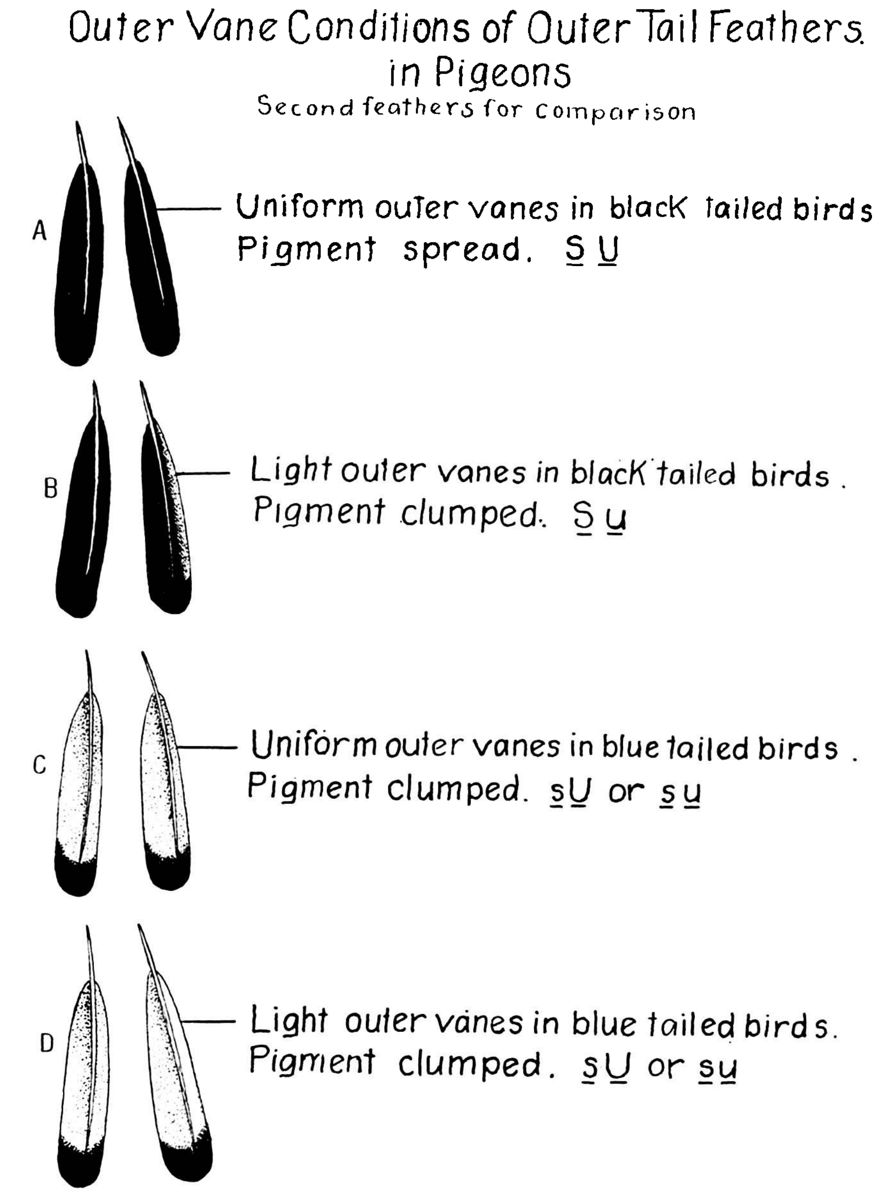

FIGURE 8.—Uniform and light outer vanes in *S* and *s* birds. Another tail feather is shown in each case for comparison.

correspond to the other tail feathers. The light condition (figure 8D) of the outer vanes of blue-tailed birds appears to be due to a diminution in the amount of pigment. The difference, then, between light and uniform outer vanes in *S* birds is due to clumped and spread pigment, while an apparently corresponding condition in *s* individuals depends upon the amount of pigment, which is clumped in both cases.

The foregoing may be explained on the assumption that a factor *U* spreads black pigment in the outer vanes of outer tail feathers of *S* birds, while *u* clumps it. Since *s* has already produced clumping in the tail region of blue-tailed birds the effect of *u* is not noticeable, and apparently *U* can not act in the presence of *s*. Still there is no reason to believe that *s* birds can not carry *U*.

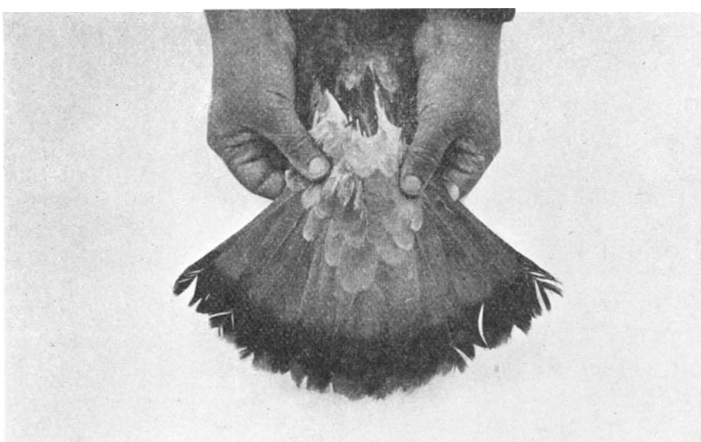

FIGURE 9.—Uniform outer vanes in a blue-tailed bird. (Wisconsin No. 1704F.)

Before taking up the data in substantiation of such a theory two points must first be considered. The first is the variation in the degrees of lightness exhibited by different individuals. This is due in both black and blue-tailed birds to differences in the amount of pigment. It may depend, also, upon the age of the birds, younger ones showing more pigment than older ones. In fact it was found from a study of the several descriptions of many individuals that the first frequently gave the outer vanes as "uniform," while later descriptions, made after the birds had moulted, often gave them as "light." This was true of both types of birds. As a consequence the left outer tail feathers were plucked from squabs of various ages to determine whether this, like a normal moult, would tend to decrease the amount of pigment in the incoming feathers.

Such proved to be the case, as illustrated in figure 10, which represents 2 and 3 plucks from twelve birds. In view of the foregoing it was necessary to use only old birds, or squabs from which one of the outer tail feathers had been plucked at least once, before compiling the tables which follow.

The second point for consideration is lightening due to factors other than u. In certain cases of black-and-white-mottled birds the outer vanes may be light but such pigment as is present is spread, which probably indicates the action of factors for white spotting. Conse-

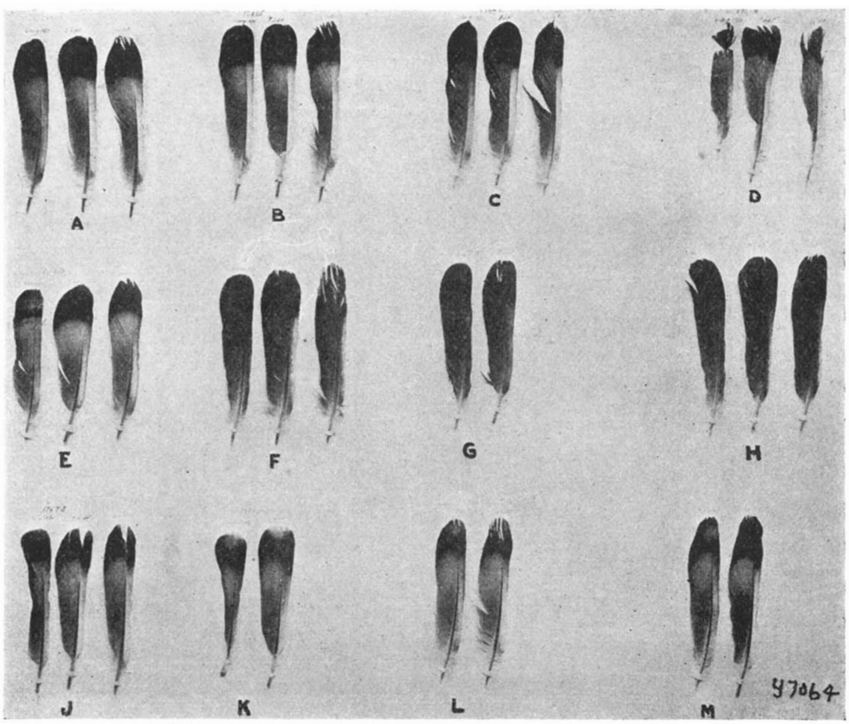

FIGURE 10.—Outer tail feathers of squabs, plucked successively upon their regrowth, showing the acquirement of light outer vanes in the later feathers.

quently in any doubtful cases a microscopic examination was necessary. The factors for white spotting are not included in the consideration of light and uniform outer vanes, but only U and u.

The dominance of UU in the presence of SS was indicated by seven matings which produced thirty-six uniform-outer-vaned offspring. The homozygous condition of U was judged from the offspring. No mating producing less than five individuals was used except in one case where the pedigrees of the parents indicated their compositions. In the other matings some of the birds were "original" and consequently were unpedigreed, while others having pedigrees showed *b* or *s* or *A* birds in their immediate ancestry, making it impossible to judge of their composition.

Other matings showed the segregation of *Uu* in the presence of *SS*. Three matings in which both parents were *Uu* produced 18 "uniform" and 4 "light" black-tailed offspring, which is, considering the numbers, fairly close to expectation (16.5 : 5.5). Two matings of *Uu* to *uu*, from which a 1:1 ratio is expected, gave 10 : 11.

If *u* is a definite factor independent of *S*, then when *SSuu* or *Ssuu* birds are bred either *inter se* or to *s* individuals of the composition *uu*, all the *S* offspring should have light outer vanes. This condition has been only partially tested. An *Ssuu* (figure 8B) bird was bred to an *s* bird with light outer vanes (figure 8D), the condition of which with respect to *U* could not, of course, be phenotypically judged. From such a mating, however, nine offspring resulted, five *S* and four *s*, all of which had light outer vanes. Three of the *Ssuu* offspring were in turn mated to light-outer-vaned *s* birds and produced 26 offspring. Fourteen of these were blacks (*S*), and all, with the exception of one which died young before the first-plucked outer tail feathers had been replaced, had light outer vanes. This showed fairly conclusively that the original bird tested was of the composition *Ssuu*. Furthermore, the *s* bird to which it was mated, also evidently lacked *U*, as did the *s* birds to which the three *Ssuu* offspring of the original pair were bred.

When, however, two *Ssuu* (figure 8B) were bred together they produced an *SU* (figure 8A) individual, which is a decided exception and no explanation for which is at present apparent. This is a weak point in the theory, for only *u* birds should have resulted. It is recognized that the data which are presented in substantiation of the foregoing hypothesis are few, and in order to further strengthen it more *SSuu* and *Ssuu* birds should be thus tested. In this event another theory might better explain the data, but with the present records the present hypothesis seems to be the most satisfactory one available.

If, as supposed, *U* is unable to act in the presence of *s*, any definite breeding behavior of so-called light- and uniform-outer-vaned *s* birds is not expected. Of 51 matings of phenotypically light-outer-vaned blue-tailed birds bred *inter se*, four threw some offspring which had uniform outer vanes (figure 8C). As already mentioned, however, the point of difference is amount of pigment, so naturally the *U* factor just postulated would have no apparent effect. These four matings refer only to those in which offspring were of a sufficient age to have passed through at least two or three moults or have had their outer tail feathers plucked several times. Seven other matings also show the production of uniform-outer-vaned offspring, but these individuals died young, and hence are not considered in this connection for reasons previously mentioned.

To show further that so-called uniformity in *s* birds is not the same as in *S* individuals, two so-called uniform-outer-vaned blue-tailed birds were bred to light ones and only light-outer-vaned offspring (16 in number) resulted. This plainly indicates that the genetic relation of the light and uniform conditions in *s* birds is complicated.

TABLE 6

Matings of SsUu birds × Ssuu birds.

MATING	♂♂	COLOR	COMPOSITION	♀♀	COLOR	COMPOSITION	OBSERVED			EXPECTED		
							SU	*Su*	*sU+su*	*SU*	*Su*	*sU+su*
554+	450X	Dun	*Ssuu*	450Y	Dun	*SsUu*	5	1	1	2.54	2.54	1.76
662+	493B	Black	*Ssuu*	454B	Black	*SsUu*	4	7	1	4.04	4.04	2.76
1047+	829B	Dun	*SsUu*	829A	Dun	*Ssuu*	1	1	1	1.14	1.14	.76
1024+	901B	Black	*SsUu*	890B	Dun	*Ssuu*	(1*)	1	1	.75	.75	.50
Total (4 matings)							10	10	4	9	9	6

* Died young, therefore omitted from consideration.

Table 6 gives matings of *S* and *s* birds from which a 3:3:2 ratio is expected. The numbers are small (10:10:4) but approach the calculated (9:9:6) rather closely. Table 7 shows thirteen matings from which if the *s* birds are *Uu* a 3:1:4 ratio is expected and if they are *uu* a 1:1:2. They are known from pedigree and offspring to be of one or other of these compositions. The closeness of fit (P) for the first of these ratios is poor but for the second, good. There are, however, doubtless both *U* and *u* birds among those which are *s*. If it is assumed that half are *U* and half *u*, the expected ratio would be 5:3:8 (3:1:4+2:2:4). The closeness of fit on this assumption is excellent, χ^2 being less than 1. The numbers are, to be sure, small and consequently not too much importance is to be placed upon them, but the ratio at least lies between 3:1:4 and 1:1:2. It may, therefore, be assumed that the *s* parents comprised both *Uu* and *uu* individuals.

In order to prove further that *s* birds carry *U*, blue-tailed individuals with phenotypically light outer vanes have been bred to *Ssuu* individuals, n which case any *SU* offspring must have gotten *U* from its *s* parent.

TABLE 7

Matings of SsUu birds × ssUu or ssuu birds.

MATING	♂♂	COLOR	COMPOSITION	♀♀	COLOR	COMPOSITION	OFFSPRING *SU*	OFFSPRING *Su*	OFFSPRING *sU+su*
826+	6A	Black	*SsUu*	639B	Silver	$ss\begin{Bmatrix}Uu\\uu\end{Bmatrix}$	1	1	4
837+	639A	Silver	$ss\begin{Bmatrix}Uu\\uu\end{Bmatrix}$	719B	Black	*SsUu*	2	1	2
1448	1341D	Blue	$ss\begin{Bmatrix}Uu\\uu\end{Bmatrix}$	915B	Dun	*SsUu*	7	1	3
1454	1385B	Black	*SsUu*	1242A	Blue	$ss\begin{Bmatrix}Uu\\uu\end{Bmatrix}$	5	1	3
1472	829B	Dun	*SsUu*	1296N	Blue	$ss\begin{Bmatrix}Uu\\uu\end{Bmatrix}$	3	2	5
1605	1341D	Blue	$ss\begin{Bmatrix}Uu\\uu\end{Bmatrix}$	1500H	Dun	*SsUu*	1	1	4
1681	1512R	Black	*SsUu*	1657Z	Blue	$ss\begin{Bmatrix}Uu\\uu\end{Bmatrix}$	......	1	3
1682	1448T	Black	*SsUu*	1668A	Blue	$ss\begin{Bmatrix}Uu\\uu\end{Bmatrix}$	......	2	7
1693	$1593C_2$	Black	*SsUu*	$1607B_2$	Check	$ss\begin{Bmatrix}Uu\\uu\end{Bmatrix}$	......	1	1
1695	1568B	Black	*SsUu*	1607U	Check	$ss\begin{Bmatrix}Uu\\uu\end{Bmatrix}$	1	1	1
1745	1638A	Blue	$ss\begin{Bmatrix}Uu\\uu\end{Bmatrix}$	1484A	Black	*SsUu*	......	1	1
1761	1455V	Blue	$ss\begin{Bmatrix}Uu\\uu\end{Bmatrix}$	1553B	Black	*SsUu*	2	2	1
1773	1568B	Black	*SsUu*	1296N	Blue	$ss\begin{Bmatrix}Uu\\uu\end{Bmatrix}$	2	1	3
Total (13 matings)							24	16	38

Expected:

	SU	*Su*	*sU+su*
1. If *s* birds are *Uu*, a 3:1:4 ratio is expected.............	28.89	9.63	38.52
2. If *s* birds are *uu* a 1:1:2 ratio is expected..............	19.50	19.50	39.00
3. If one-half of the *s* birds are *Uu* and the other half *uu*, a 5:3:8 ratio is expected..........................	23.35	14.61	38.96

1. $\chi^2=5.0443$	P=.0806
2. $\chi^2=1.178$	P=.5620
3. $\chi^2=.173$	....

Of some twelve birds tested seven have been found to be *SU*, which upholds the above presumption. There are two matings on which data are lacking because in each an *S* squab died before the replacement of the first plucked feather.

Evidently there is a decided interaction of *S*, *U*, and their allelomorphs. *S* permits of the phenotypic expression of both *U* and *u*, while *U* can not express itself in the presence of *s*. Since both *u* and *s* produce the same effect, namely a bluing due to clumped pigment, they are indistinguishable

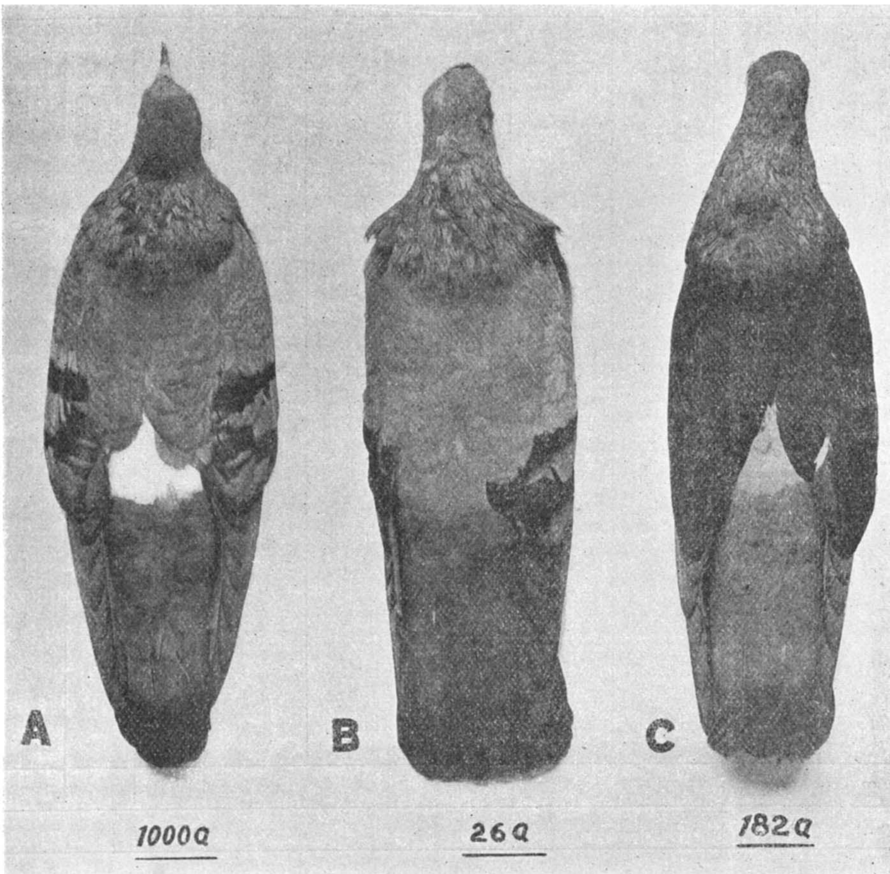

FIGURE 11.—A. Extreme light rump (grade 1) in blue black-barred wild Rock pigeon. (Wisconsin No. 1000A.) B. Uniform blue rump (grade 3) in blue black-barred common pigeon. (Wisconsin No. 26A.) C. Very slight check with light blue rump (grade 2). (Wisconsin No. 182A.)

when combined. No definite factor was found for the difference in amount of pigment in the outer vanes of *s* birds.

LIGHT AND UNIFORM RUMP

The two rump colors "white" and blue, found respectively in *C. livia*, particularly common in Europe, and *C. intermedia* of India, have long attracted the attention of naturalists. This is the one mark of differentiation between these two species. According to Salvadori (1893, p. 255), however, some specimens of *C. livia* may have the blue rump, in which cases they are indistinguishable from *C. intermedia*. In fact Salvadori (p. 256) states that "every ornithologist knows the difficulty of drawing the exact line between *C. livia* and *C. intermedia*." This question is discussed in some detail by Darwin (1868) and others already cited. The former attributes the difference in color of these two types to climate, the warmer environment of India tending to produce a color uniform with the rest of the bird.

"White" and blue rumps (figures 11A and 11B), together with many intermediate shades, also exist in barred and checked birds of several varieties of domestic pigeons. A detailed examination of many birds of the intense series admits of three fairly definite categories. Only intense individuals were used, as those of the dilute series presented another, but presumably strictly parallel, range of much lighter shades which were more difficult to classify.

The first or lightest grade is the "white" rump, typical of *C. livia*. This is preferably termed "extrème light blue" because a microscopic examination shows the presence of a small amount of clumped pigment, while white implies the absence of any pigment. The first grade is indicated below as number 1.

s Blue-tailed	1. Rump extreme light blue—typical of *C. livia* (figure 11A). 2. Rump light blue—several shades of light blue (figures 5 and 6). 3. Rump uniform blue—typical of *C. intermedia* (figure 11B).
S Black-tailed	4. Rump dark blue—found in some black birds (figure 12). 5. Rump black—uniform with the rest of the plumage (figure 1).

The next grade (number 2), found very frequently in general stocks of pigeons, is light blue. This color is not suggestive of white but of a silvery blue. Furthermore, the range of shades in this class is rather wide, extending from a very light blue, distinct from grade 1, to a shade just perceptibly lighter than uniform blue, grade 3. Uniform blue, as suggested in the first paragraph, refers to the correspondence in shade between rump, back and wing coverts. The pigment is clumped in grades 1, 2 and 3. The amount of pigment is apparently the determiner of the various shades, the lighter ones having less pigment than the darker. There are, then, at least three color-grades of rump in the *s* or blue-tailed birds, depending upon the amount of clumped pigment.

A consideration of rump conditions in black-tailed birds reveals two fairly definite types. Certain *S* individuals may be solid black except for a lighter shade of rump, the feathers of which give a dark blue appearance, (grade 4). It is a darker blue than any above described. The pigment, however, is clumped as it was in each of the foregoing cases. This grade, like the light blue (2), shows some range in shade, but for present purposes these shades will all be considered together under 4.

The last type (grade 5) occurs in *S* individuals and refers to a black rump uniform with the rest of the black plumage. In this case the pigment is spread.

These conditions are analogous to those found in the outer vanes of outer tail feathers of both blue- and black-tailed birds. In both cases the pigment is clumped in *s* birds and the shade depends upon the amount of pigment present. The dark blue rump of black birds corresponds to the light condition in the outer vanes of *S* birds in that the pigment is clumped, while the black rump and uniform outer vanes both have spread pigment.

The genetic analysis of the rump conditions is, however, more difficult than that of the outer vanes. The work of STAPLES-BROWNE (1908, 1912) is, so far as the writer is aware, the only report on the definite inheritance of these characters. His records are based on breeding tests of *s* birds only. Extreme-light-blue rump (1) appears to be dominant to uniform-blue (3), to segregate fairly cleanly, except for the appearance of some light blues (2), and uniform blue breeds true. He classes the light blues (2) with the uniform blues (3). WHITMAN (1919, vol. 2, table 87c, p. 112) obtained a uniform-rumped individual from a pair of presumably extreme-light-blue-rumped (1) wild *C. livia*.

The writer has collected considerable data from many matings and in certain cases obtained results corresponding to those of STAPLES-BROWNE. When, for instance, extreme-light-blue-rumped (1) birds were bred to light-(2) or uniform-blue-rumped (3) ones, all three types resulted. From fourteen matings of uniform-blue rumps (3), bred *inter se*, types 2 and 3 resulted, while one such mating also produced grade 1. This latter case is not in keeping with STAPLES-BROWNE'S findings. The writer's data correspond to those of STAPLES-BROWNE in that types 1 and 3 do not segregate cleanly when crossed, but produce light blue rumps (2). As previously stated STAPLES-BROWNE considered these latter as uniform blues (3). It has been found, however, that the light shades, when bred together or to uniforms, throw extreme-light-blue-rumped (1) offspring as well as uniform (3)- and light-blue (2)-rumped individuals.

In view of these discrepancies the writer made another classification for all matings,[8] including types 1 and 2 under one head and type 3 under the other, whereas STAPLES-BROWNE made one class of type 1 and combined 2 and 3. On such a basis as the former, that is, making a single class of 1 and 2, and one of 3, results are equally confusing. When extreme (1) or light (2) blues heterozygous for (3) are bred together, all three types result in a proportion of 3 : 1 (37 : 13), types 1 and 2 being combined to form the larger class. If heterozygotes, grades 1 and 2, carrying 3, as indicated by pedigree, are crossed on grade 3, the assumed recessive, the results of thirteen matings show 30 : 54 in the respective classes, that is, twice as many recessives as dominants. Type 3 does not breed true, but produces as many extreme and light blues (1 and 2) as uniform (3), the numbers being 37 : 39 from 14 matings. Obviously, then, this scheme comes no nearer to explaining the inheritance of rump conditions in *s* birds than did that of STAPLES-BROWNE.

Further instabilities are encountered when the breeding behavior of the dark blue (4) rump of black birds is considered. As already mentioned STAPLES-BROWNE's data related to *s* birds only. Dark-blue-rumped (4) *S* offspring may be obtained from light(2)- or extreme-light(1)-blue-rumped birds, crossed on black-rumped (5) blacks. When these dark blues (4) are mated together they may produce a very small proportion of individuals like themselves (1 in 21 offspring), and they may throw some light (2) *s* offspring. Three matings of type 4 by type 2 produced all five types. Similarly, when grade 5 is crossed on grade 3 (24 matings) the five types result. If, on the other hand, black rumps (5) are mated to black rumps (17 matings) an occasional grade 2 may appear, but the majority belong to grade 5.

Evidently the inheritance of the various rump conditions in blue- and black-tailed birds is due to a complicated interaction of factors. In order to obtain the correct genetic analysis more detailed breeding experiments must be undertaken.

THE RELATION OF THE DULL-BLACK CHECK TO DEEP AND DULL BLACK

The modifications of black dealt with so far have been due to the relative amounts of the so-called colors, blue and black, exhibited by certain

[8] Only those birds for which rump feathers have been saved or the descriptions record "Rump lighter than wing coverts," or "Rump same shade as wing coverts," have been used in these tables.

individuals, or in other words to the encroachment of clumped pigment upon spread. There is another diversity of black of another sort in that it does not involve bluing but is a modification of the depth and sheen of the color of many black birds. Some individuals may have either a brownish or a powdery plumbeous cast instead of a deep uniform velvety one. These conditions are considered undesirable by breeders of black varieties of pigeons. CHAPMAN (1911) calls attention to them as "very grave defects."

Furthermore, some of these birds may show darker indistinct wing bars in the usual position (figure 13) or in some cases check marks lighter than the general color in the wing coverts (figure 12). These are due to two shades of black instead of the usual blue and black of the epistatic series described in earlier sections of this paper. BOITARD and CORBIÉ (1824)

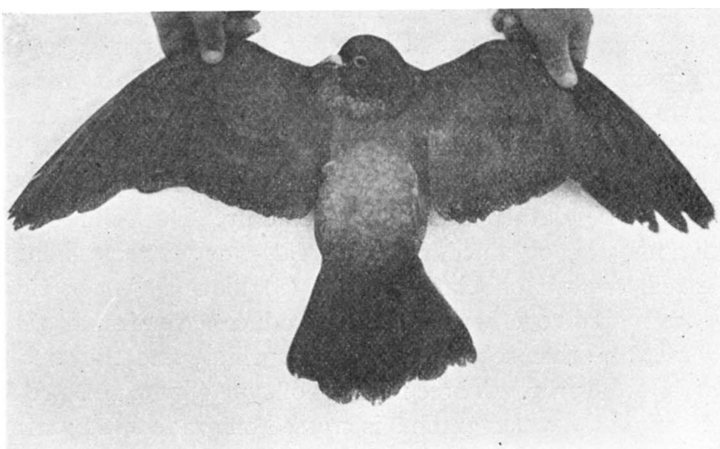

FIGURE 12.—Dull black check with dark blue rump (grade 4) and light outer vanes of outer tail feathers. (Wisconsin No. 1827C.)

mention the cropping out of indistinct wing bars on black birds in certain crosses.

Checks and bars of this description are likewise prevalent among duns (dilute blacks). The two main differentiating points between checks of this type, that is, dull-black or dun, and the blue type, are, first, the absence of the typical blue or silver tail with a black or dun terminal band, and second, the production of checks and bars by two shades of black or dun, and not by black and blue or dun and silver. In other words these checks and bars carry *S* while the blue type does not. These two points are further emphasized when the pigment-granule arrangement is studied, for all pigment in the dull-black or dun checked birds is in a spread condition. It is, however, more dense in the wing bars and darker areas surrounding the check marks than in the checks themselves and regions about the wing bars. The deeper-colored areas correspond to the black of barred and checked birds of the blue-black epistatic series, while the lighter areas correspond to the blue color.

Unfortunately breeding data on these patterns are very few. There are, however, several matings which give the breeding behavior of dull black (d) without bars or checks as contrasted to deep black (D). The chief distinguishing characteristics between this factor and I which affects density are (1) D is not like I in being sex-linked, (2) the difference in shade between d and i birds is readily distinguishable and (3) so far as is known at present, d individuals are indistinguishable from D in the presence of i.

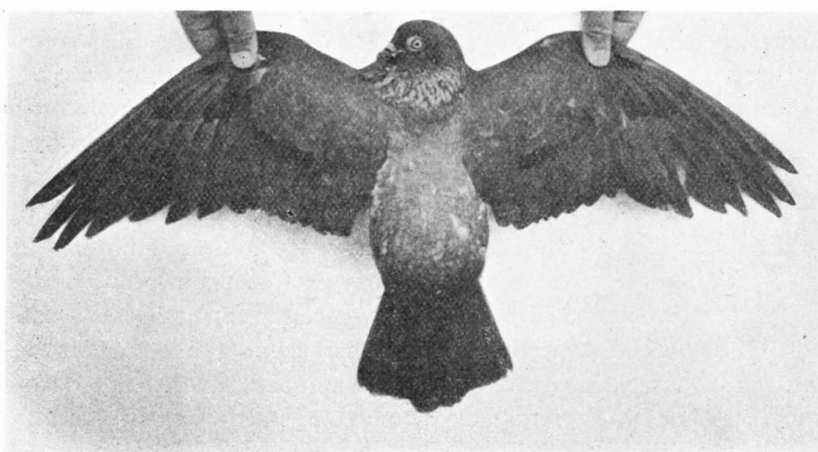

FIGURE 13.—Dull black with blacker bars, uniform rump (grade 5) and light outer vanes of outer tail feathers. The light appearance of the rump is not due to bluing but to a very dull black. (Wisconsin No. 1761J.)

The data on the relation of d and D in blacks are presented, because, to anticipate a little, it seems evident that the d condition is necessary for the manifestation of the two patterns. D does not permit of the presence of any contrasting shade or color, for birds carrying it are deep blacks uniformly pigmented.

This character, like that of the outer vanes of the outer tail feathers, changes with age. Most if not all black squabs are dull, and not until they have moulted at least once does the deep plumage, if they are to have that as adults, appear. Accordingly only adults are considered in the following discussion.

Certain black Baldheads and self-black Tumblers that have been used in this work have had the desirable deep-black feathering. Two matings of such black Baldheads produced four offspring deep-black like their parents, indicating that one or both of the parents were homozygous for *D*. Three matings of "original" deep-black Tumblers bred to deep-black checks gave a different result. "Checks" in this connection refers to the blue or *sC* check, in which the black can be either dull or deep. Since the Tumblers were original birds their genotypic compositions were unknown. The checked parents were, however, from colony stock and known to be *Dd*. As both deep and dull blacks were produced it was concluded that the Tumblers were likewise heterozygous. There were 12 of the former and 8 of the latter, where a 3:1 ratio was expected.

As just mentioned, the checks employed here refer to the *sC* of the epistatic series. Since such individuals present both blue and black, obviously the shade of black can be determined providing the black area of the wings is large enough, that is, if it occupies as much space on the wings as does the blue. A fairly large black region is necessary in order to admit of comparison. This was further emphasized when an attempt was made to compile data on the shade of black from bars and extreme checks. This was found impossible. As a consequence only blacks, black blue-rumps and slight to medium checks are used in these tables.

Table 8A shows six matings of heterozygous deep blacks bred to dull blacks, giving 14 deep to 11 dull blacks where the expected is 12.5:12.5. Section B shows the same thing except that some of the parents are *sC* checks. In this case the results are 14:16 and the expected is 15:15. A total for the 14 matings gives 28 to 27 where equality is anticipated.

Thirteen matings of dull to dull demonstrated the true-breeding behavior of this character, forty-four dull and no deep offspring being obtained. Obviously, then, the difference between dull and deep black is a single factor.

As previously mentioned, it is fairly apparent that *D* birds can not display the dull-black check and bars, because this would necessitate the introduction of poor black in deep-black individuals, which very evidently is not in keeping with the deep-black character. If this is the situation the present type of check, like the blue of the epistatic series, is due to an interaction of factors. That is, *d* is necessary for its manifestation as *s* is for that of the blue check, but the former carries *S* while the blue type lacks *S*. In the former respect the *s* and *d* conditions are analogous. The two checks may be termed the *sC*, typical of *C. livia*, and the *dS*, that just described.

TABLE 8

*Deep black (Dd) by dull black (dd).**

MATING	♂♂	COLOR	COMPOSITION	♀♀	COLOR	COMPOSITION	OFFSPRING D	OFFSPRING d
A. Blacks by blacks								
120+	45B	Deep black	*Dd*	56A	Dull black	*dd*	4	1
575+	448A	Deep black	*Dd*	432B	Dull black	*dd*	1	1
835+	719A	Dull black	*dd*	727A	Deep black	*Dd*	3	7
1317	1015B	Deep black	*Dd*	1127B	Dull black	*dd*	2	
1812	1685C	Deep black	*Dd*	$1594Q_3$	Dull black	*dd*	4	
1826	$1574F_2$	Deep black	*Dd*	1594R	Dull black	*dd*		2
Total (6 matings)							14	11
Expected							*12.5*	*12.5*
B. Black by check and check by check								
168+	28B	Dull black	*dd*	71A	Deep black check	*Dd*	4	5
1153+	972A	Deep black check	*Dd*	559A	Dull black check	*dd*	1	1
1346	972A	Deep black check	*Dd*	1033H	Dull black	*dd*		1
1684	1665A	Deep black check	*Dd*	1677A	Dull black	*dd*		1
1692	$1553J_2$	Dull black	*dd*	1616X	Deep black check	*Dd*	4	3
1693	$1593C_2$	Deep black	*Dd*	$1607B_2$	Dull black check	*dd*	1	
1695	1568B	Deep black	*Dd*	1607U	Dull black check	*dd*	1	1
1699	1657K	Deep black check	*Dd*	1605V	Dull black	*dd*	3	4
Total (8 matings)							14	16
Expected							*15*	*15*
Total for 14 matings							28	27
Expected							*27.5*	*27.5*

* Only adult birds considered.

CHECK MARKINGS IN THE COLUMBIDAE

The preceding evidence leads to the conclusion that the domestic pigeon presents two types of checks and bars, due to the interaction of at least three different factors, and varying in pigment-granule arrangement and density of pigmentation. It was pointed out in the introduction that there were several species closely related to *C. livia* which resembled the barred form and one or two the checked. These also correspond to the same patterns in the domesticated pigeon. The dull-black check described in the preceding section for domesticated varieties is a regular marking in *C. guinea*, closely related to *C. livia*. The check marks, which are V-shaped and situated at the tips of the wing coverts, are lighter than the surrounding areas, but the pigment is, in general, spread in all parts of the feathers. There is, however, a tendency to clump near the tips of the barbules, especially in the region of the V-shaped check mark.

These two types are found only in those forms closely related to *C. livia*. But there is another check condition which obtains in certain species outside the Columba group. In these the check marks instead of being lighter than the surrounding areas, as is usual in both the blue and dull-black checks, are darker than the rest of the plumage. Examples of this type are to be found in the mourning dove (*Zenaidura macroura carolinensis*) and the European turtle dove (*Turtur turtur*). In the former the few checks are located in the region of the usual wing bars of *C. livia*, and are black against the surrounding brown plumage. The dark checks of the turtle dove occupy the entire centers of the wing coverts, which are edged with a lighter shade.

Sufficient breeding data relating to the inheritance of this type of check are lacking. Microscopic examinations have been made, however, of the feathers of several individuals representing various species chosen at random. In all cases the pigment was spread throughout the feathers but was more dense in the dark check marks than in the lighter surrounding areas. This is just the reverse of the dull-black check, in which case the check is lighter than the rest of the feather, being the area of lesser pigmentation. It will be noted that in both cases all the pigment is spread, the differentiation of the pattern being based on density of pigment and not on arrangement of granules. The forms in which this condition was studied were *Zenaidura macroura carolinensis*, *Turtur turtur*, *Turtur lugens*, *Columbigallina rufipennis*, *Geopelia striata* and *Oena capensis*.

GENERAL DISCUSSION

The work by COLE (1914) and the present work on blue and black color in pigeons deal with two types of interacting factors. Both are dependent upon B[9] for their phenotypic expressions. All the factors of the first group, belonging to the epistatic series, produce similar effects, namely, clumping and spreading pigment. Each, however, is limited in its action

[9] See footnote 6, p. 486.

to a particular region. For example, the factor for barring, B_a, spreads pigment in the wing-bar region, that for sooty, S_o, introduces a sprinkling of black color in the wing coverts, which may acquire definite black spots resulting in a checked appearance when C, the checking factor, is added. In this case the sooty areas become distinctly black by the addition of more spread pigment. Similarly, the effect of the checking factor is concealed by the full spreading of black to the wing coverts leaving either a blue rump and tail or only a blue tail, when T is present. T in turn is hidden by S, which spreads pigment throughout the plumage of the individual, making it a solid black. The epistatic series, then, consists of a set of factors each of which increases the area of spread pigment over that of its predecessor. Or, in other words, the respective dropping out of each of the several factors is necessary for the phenotypic expression of those lower in the series.

The factors of the second group, namely, those for uniform and light outer vanes of outer tail feathers, uniform and light rump, and deep and dull black, are dependent upon B and S for their various expressions. They do not, however, lie in the epistatic series but interact differently. U, for uniform outer vanes of outer tail feathers, can express itself only in the presence of S, being indistinguishable in all s birds.

The several rump conditions vary somewhat similarly in black- and blue-tailed birds. Dark blue rumps are known to exist in S birds. They might, however, be found in the extreme type of black blue-tails (sT) in which ordinarily the tail is blue and the rump black like the wing coverts. This is pure supposition, as no birds of this description have been identified. Below these the rump colors change to those described for s birds.

Both I and the higher stages of the epistatic series, S, T, and some grades of C, are necessary for deep and dull black to make themselves apparent.

There are, then, two types of interacting factors, those of the epistatic series behaving in an orderly serial fashion, and others which are dependent upon certain stages of the series for their various expressions.

With the isolation of the several factors of the epistatic series comes the fact that the previously postulated ratios between S and s birds are changed. For example, it was pointed out above (p. 480) that COLE (1914) considered all checks (only checks were involved in the three illustrative matings used by him, no black blue-tails or sooties) as blacks and consequently he expected three blacks and checks to one barred. Since, however, the existence of the checking factor has been determined, the former 3:1 ratio becomes a 15:1, as two factors instead of one are involved. If, on the other hand, the present interpretation is correct, blacks heterozygous for S when bred *inter se* should give a 3:1 ratio, considering black blue-tailed birds and all individuals below them in the series as s. The combined available data fit this ratio well, with the observed numbers 71:28 and the expected 74.25 : 24.75. The probable error (P.E.) of the ratio is .12 and the $\frac{\text{Dev.}}{\text{P.E.}}$ is 1.08. Similarly, in the data giving an expected 1:1 ratio the total observed were 43:55 and the expected 49:49. The P.E. in this case is .068 and the $\frac{\text{Dev.}}{\text{P.E.}}$ is 1.47. These results are in keeping with the present hypothesis.

Unless some stage shall be found that is dependent upon S, the ratio between S and s will continue to remain the same. If, however, more intermediates involving both S and s should later be isolated, the various ratios existing between the present known factors will become altered. It seems, furthermore, highly probable that more factors are concerned, since the series appears to grade from black through to a pure blue wing lacking any black except that confined to the tips of the primaries, secondaries and tertiaries. If six grades in this series have been shown to exist independently, there is no reason why others could not also be split off, for students of Drosophila have found seven modifiers acting on one eye color alone, eosin, which in its turn lies in the graded multiple-allelomorph series from red to white.

As the members of the epistatic series increase, the chances for the occurrence of the recessives, especially those lower in the series, as the barred type, decrease. In fact, with the series as it now is, sooties and bars should appear rather infrequently if all the intermediate factors were involved. This, however, is not the case, but in several instances the number of barred birds, especially, is high. This is due, no doubt, to the fact that most of the birds making up the parents of the various matings are not heterozygous for all the characters under consideration, but for only one or two. In such a case more recessives of these types, are expected.

That the check series seems to grade almost imperceptibly from one type to another and is epistatic, is quite in keeping with WHITMAN'S selection experiments. He was able to select for less check but not for more. These results led him to believe that the evolution of checks and bars was an indistinguishable and gradual one moving in one direction. It does not, however, necessarily follow that because the interaction of these several factors produces an apparent epistatic series, the mutations producing the various grades of spread pigment occurred in any particular order. This is made even more unlikely by the fact that these factors are apparently independent and hence exist at different places in the germplasm.

The isolation of some of these factors, as particularly that for check, and a study of the various rump conditions are of interest not only from the evolutionary standpoint but also from the systematic. Certain characters governed by these factors have been used as marks of distinction between species. As pointed out earlier, SALVADORI admits that rump color is the only tangible difference between *C. livia* and *C. intermedia*. In the case of checks and bars in the wild Rock, DARWIN suggested that these two forms should be considered as a single species. He even went further and stated that several other species as *C. rupestris*, *C. schimperi* and *C. gymnocyclus* should also be included with *C. livia*. In view of the present knowledge of Mendelism, DARWIN'S suggestions are even more valid, since in certain of these cases at least, it seems evident that the species differences are based on a single factor. WHITMAN'S classification of *C. affinis*, which is checked, and *C. livia*, which is barred, illustrates this point.

Here the difference is presumably due to a single factor, C. If such marks are used for species differentiation, then the color variations of each variety of the various breeds of pigeons might as legitimately be assigned species names.

It seems possible, therefore, in view of the foregoing and the close resemblance in descriptions given by SALVADORI, of the species closely related to *C. livia*, that the domesticated pigeon may be, as suggested by GHIGI (1908), of polyphyletic origin and not descended from a single species, *C. livia*.

SUMMARY

1. The present paper is a study of several interacting factors which produce varying amounts of black and blue color in pigeons.

2. The basic factor concerned is B, producing black pigment.

3. The first group of factors consists of five which belong to the epistatic series. The lowest is B_a, spreading black pigment in the wing bars; the next is S_0, which produces a sprinkling of black in the wing coverts; the third is the checking factor, C, producing the well known check pattern; the fourth, T, spreads black throughout the wing coverts, leaving a blue tail,—this is the black blue-tail pattern; S is the highest member of the series, spreading black pigment throughout the tail, thus producing a full-black.

4. The inheritance of C has been amply proven, while that of the other factors is only indicated. All, however, have been shown to lie in an epistatic and not in a multiple-allelomorph series.

5. A factor U and its allelomorph determine uniform and light outer vanes in S birds, being indistinguishable in the presence of s.

6. Five rump conditions studied in black- and blue-tailed birds have been found to be due to a complicated interaction of factors independent of the epistatic series.

7. The density of black pigment is due to a single Mendelizing factor, D. This differs from I in that it is not sex-linked, and the shades of black resulting from it are not as light as the darkest duns.

8. A check and barred pattern due to two shades of black or dun and not to black and blue or dun and silver have been found to occur when d is present. The inheritance of these patterns has not been worked out.

9. The orderly fashion of behavior of the members of the epistatic series led WHITMAN to believe that checks and bars developed orthogenetically.

10. The orderly behavior of these factors is no criterion that the mutations producing them occurred in the same order.

11. If closely related species are found to differ from each other mainly by heritable color factors, they might on such a basis be included in a single species.

The writer wishes to acknowledge her gratitude to Professor COLE for his encouragement and helpful suggestions given during the progress of the work detailed in the preceding pages; to Dr. OSGOOD of the FIELD COLUMBIAN MUSEUM, for permission to examine the specimens of pigeons in his custody at the Museum; and to Mrs. WALDECK of Milwaukee for the loan of the blue barless Homer used in one of the matings.

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